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RESEARCH PAPER

CLASSIFICATION OF EUROPEAN FORESTS

Compositional and ecological diversity of Cansiglio forest (Friuli Venezia Giulia, Italy)

Flavia Sicuriello[1], Fabrizio Ferretti[2], Paolo Colangelo[1], Bruno De Cinti[1]

1 *Research Institute on Terrestrial Ecosystems, CNR National Research Council, Rome, Italy*

2 *Council for Agricultural Research and Agricultural Economy Analysis, CREA SEL Research Centre for Forestry, Arezzo, Italy*

Corresponding author: Flavia Sicuriello (flavia.sicuriello@cnr.it)

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Abstract

Aim: The aim of this study is to describe the compositional and ecological diversity of the Natura 2000 Site 'Cansiglio Forest' (IT3310006). **Study area:** The study area is located in the South-Eastern Prealps between the Venetian-Friulian plain and the Cansiglio plateau, a typical karstic system. **Methods:** A total of 25 vegetation relevés, each of 250 m^2, were sampled in the LIFE SPAN (LIFE19 NAT/IT/000104) project plots and were subjected to cluster analysis (Bray-Curtis, Ward) and NMDS ordination. Variables such as Ellenberg Indicator Values, environmental parameters, life forms, chorotypes, and phytosociological units were tested using ANOVA and the Kruskal-Wallis test to assess significant differences between clusters. The *indicspecies* package was applied to study the association between species patterns and combinations of clusters. **Results:** We distinguished three clusters. Cluster A, characterized by several species, including *Chaerophyllum hirsutum* and *Phegopteris connectilis*, shows higher EIVs for moisture, acidic soil reaction and lower temperature, a more open canopy and mainly Circumboreal and Euro Asian species of *Vaccinio-Piceetea*. Cluster B1, a mixed forest of *Fagus sylvatica* and *Abies alba* with *Circaea alpina*, has intermediate EIVs, a closed canopy, low herbaceous layer cover, and higher cover of SE-European species. Cluster B2, a pure *Fagus sylvatica* forest with *Lathyrus venetus*, has lower EIVs for humidity and higher for temperature, and mainly Central European species of *Carpino-Fagetea*. **Conclusion:** The anthropogenic spruce forest is developing in the Cansiglio plateau and is favored by thermal inversion. It could be identified with *Senecioni cacaliaster-Piceetum*, but further study is needed to confirm. The mixed forest of *Fagus sylvatica* and *Abies alba* and the pure beech forest represent two facies of the *Cardamino pentaphylli-Fagetum fagetosum*, with the first one dominating on the coldest slopes and the second one on the highest and warmer belt. This community can be included in the *Aremonio-Fagion* alliance.

Taxonomic reference: Euro+Med PlantBase (2023).

Syntaxonomic references: Mucina et al. (2016) for classes, orders and alliances; Willner et al. (2017) for suballiances.

Abbreviations: ANOVA = analysis of variance; EIV = Ellenberg indicator value; FVG = Autonomous Region of Friuli Venezia-Giulia; HSD = honestly significant difference; NMDS = non-metric multidimensional scaling.

Keywords

Abies alba, *Fagus sylvatica*, Illyrian species, karstic morphology, *Picea abies*, South-Eastern Prealps, thermal inversion

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Introduction

The Cansiglio Forest spans two regions in North-Eastern Italy, Veneto and Friuli Venezia Giulia, and is known for its historic forest management, which began in 1548 by the Republic of Serenissima of Venice for the manufacture of boat oars (Cassol et al. 2013). Following the establishment of the Autonomous Region of Friuli Venezia Giulia (FVG) in 1966, ownership of the forest was divided between the two regions.

The Cansiglio plateau is a typical karstic system, known as a *polje* (from Slavic languages "field"), which appears as a vast plain bordered by a crown of mountains with squared and very steep sides. The entire system emerges from the Venetian-Friulian plain, in the orographic unit of the South-Eastern Prealps. In the bottom of the Cansiglio plateau the *Picea abies* forest develops, while climbing along the rugged slope of the Friulian side the *Fagus sylvatica* forest mixed with *Abies alba* occurs, and, still proceeding upward until the subalpine plane is the terminal pure *Fagus sylvatica* forest (Figure 1) (Mayer and Hofmann 1969; Del Favero et al. 1998). Among the hypotheses explaining this inverted vegetation series, the most noticeable phenomenon is thermal inversion, which results in a stagnation of cold moist air favoring *Picea abies* at the bottom (Busato and Lorenzoni 1973; Pignatti 1998).

Another peculiar element of this forest is its marginal position on the boundary of the Friulan-Venetian plain, which exposes the higher parts to the moisture currents, setting up a distinctly oceanic climate that is the optimum for *Fagus sylvatica*. Further inland, decreasing precipitation and increasing continentality favor the presence of *Abies alba* and *Picea abies*, a phenomenon that seems to be more important than the increase in elevation, as occurs in the North of the Alps (Poldini and Vidali 1993).

The South-Eastern Prealps saw the growth of the *Picea abies* population in the late glacial period, which then spread to the inner Central Alps and later to the Western Alps (Magri et al. 2006). Previous studies carried out in the Palughetto mire report the presence of forests with *Picea abies* in the Cansiglio plateau since 14,600 years BP (Vescovi et al. 2007). Concerning the recent history of the forest communities at the valley bottom, silvicultural treatments favoring *Picea abies* have been quite intensive (Vitale and San Martini 1914; Hofmann 1931) and, as in the case of the inner Alps (Gafta 1994), have led to the formation of an anthropogenic forest which is difficult to fit into a syntaxonomic scheme (Poldini and Bressan 2007).

Regarding *Fagus sylvatica* forests, studies carried out in the Palughetto mire suggest that *Fagus sylvatica* was present in the Cansiglio Forest since at least the early Holocene, but it became more abundant only during the

Figure 1. Panoramic photograps of Cansiglio Forest. **Left side**: vegetation belt (from the bottom) *Picea abies*, mixed *Fagus sylvatica* and *Abies alba*, pure *Fagus sylvatica* communities. **Top-right**: moist air on the top of Cansiglio forest. **Bottom-right:** stagnation of cold moist air in the Cansiglio plateau.

mid-Holocene (Vescovi et al. 2007). The increase in *Fagus sylvatica* abundance during the mid-Holocene is thought to be related to the cooling and moistening of the climate, which favored the expansion of beech forests in the European Alps (Tinner and Lotter 2006).

The Cansiglio Forest is part of a larger region that extends from the Northern Apennines to the North-Eastern Dinaric mountains and is characterized by a high diversity of *Fagus sylvatica* forests (Willner et al. 2009). The Southern-Eastern Alps likely represent a migration route from Northern Apennines and the Dinaric Alps refugia during the last glacial period (Magri et al. 2006; Willner et al. 2009).

The presence of Illyrian species, which are endemic or subendemic to the Illyrian region (Trinajstić 1992; Poldini and Galizia Vuerich 1997), has led some authors to frame this community within the suballiance *Saxifrago rotundifoliae-Fagenion* and the alliance *Aremonio-Fagion* (Marinček et al. 1993; Poldini and Nardini 1993; Poldini and Vidali 1993; Marinšek et al. 2013). This hypothesis would also be supported by the analysis of the degradation stages of the submontane, montane, and subalpine horizons, which lead to replacement herbaceous associations that also fall within Illyrian syntaxa (Chiapella Feoli and Poldini 1993). It must be said that some authors do not consider the Illyrian species to be sufficient for framing these communities within the *Aremonio-Fagion*, instead placing them in the more central *Fagion sylvaticae* (Pignatti and Pignatti 2016). Another aspect that is not yet completely clear at the syntaxonomic level is the identification of the communities of *Fagus sylvatica* mixed with *Abies alba*, which are known among foresters as '*Abieti-Fagetum*'. Some authors frame this community as an association in its own right as *Cardamino pentaphylli-Abietetum* Mayer 1974 (Gafta 1994; Poldini and Bressan 2007), while others consider it to be a facies of *Cardamino penthaphylli-Fagetum* (Poldini and Nardini 1993).

The aim of this study is to contribute to the knowledge of the compositional and ecological diversity of forest plant communities, with some suggestions on syntaxonomy, of the Natura 2000 Site 'Cansiglio Forest' (IT3310006).

Methods

Study area

The study area (Figure 2) is located in the 'Foresta del Cansiglio', mainly in the Natura 2000 Site (IT3310006) (https://eunis.eea.europa.eu/sites/IT3310006) in North-Eastern Italy. The reserve covers approximately 2,713 ha, 88% of which is forest, and is managed by the FVG (Cassol et al. 2013).

The bedrocks consist of limestone and marl of the Monte Cavallo formation (Mantovani et al. 1976), which

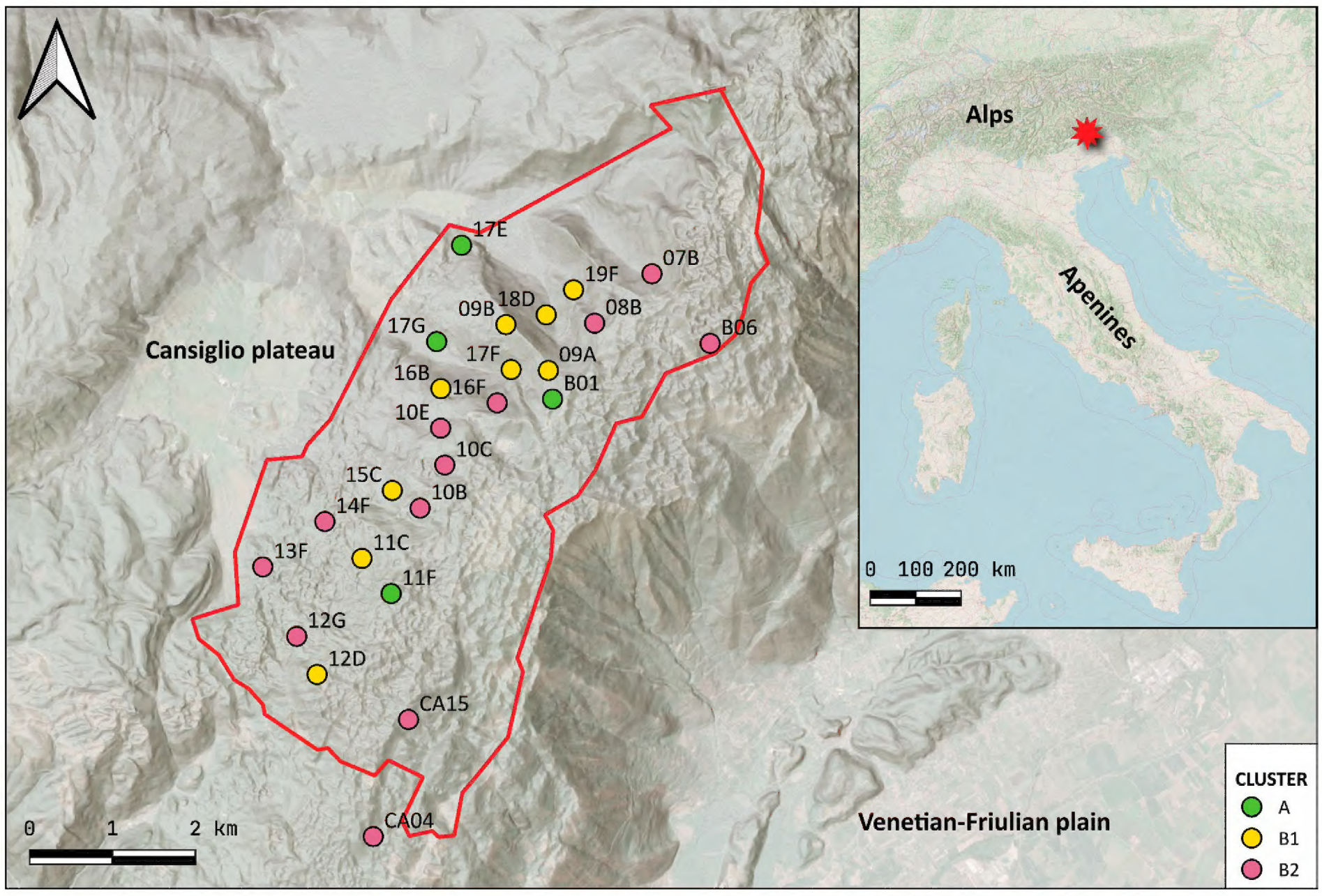

Figure 2. Study area. Perimeter of Foresta del Cansiglio Natura 2000 Site (IT 3310006) in red line and location on Nord East of Italy. Dots in the maps represent the relevés locations, colors according to clusters: **A** *Picea abies* community. **B1** *Fagus sylvatica* with *Abies alba* community. **B2** *Fagus sylvatica* community. Maps based on OpenStreetMap (OpenStreetMap contributors 2015)

were deposited in the marine environment of a carbonate reef during the Middle-Upper Cretaceous. The inner plateau of Pian del Cansiglio develops in a Northeast-Southwest direction at an average altitude of about 1000 m a.s.l., while the surrounding mountain crown culminates in Monte Pizzoc (1565 m a.s.l.) and Millifret (1581 m a.s.l.) to the South-West and in Monte Croseraz (1694 m a.s.l.) and the Monte Cavallo group (2250 m a.s.l.) to the North-East. The karst phenomena create numerous cavities, caves, and sinkholes, and they do not allow the development of a superficial hydrographic network. Only in some sinkholes does waterproofing due to the accumulation of clay minerals cause water stagnation.

For climate data, we refer to a historical series from the years 1994 to 2022 from the weather station of 'Cansiglio-Tramedere (TV)' operated by ARPAV (2023) and located at 1022 m a.s.l. on the Cansiglio plateau (Figure 3).

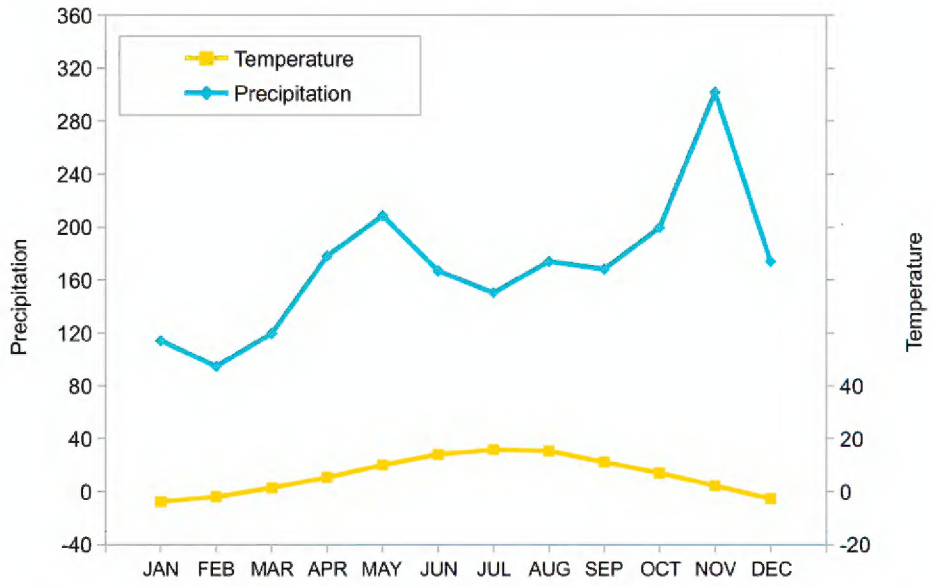

Figure 3. Average monthly temperatures as Celsius degree and precipitation as mm for the years 1994–2000 of Cansiglio – Tramedere station, Veneto, Italy.

The average annual precipitation recorded for the period is 2050 mm, with an average annual temperature of 6.1 °C. The precipitation data show a maximum in November and two other attenuated peaks in May and August. In the Cansiglio plateau, thermal inversion is a common phenomenon in which cold, denser air from the marginal reliefs gets trapped in the valley floor, which has an average altitude of 1015 m. This phenomenon is attributed to the higher elevation of the Crosetta (1120 m) and Campon (1050 m) passes, which hinder air from exiting the plateau. Consequently, this can result in negative temperature peaks of -30 °C during the winter season, causing prolonged snow cover and frequent fog formation (Cassol et al. 2013).

Regarding the edaphic conditions (Garlato and Borsato 2016), the plateau is characterized by Cutanic Alisols (FAO 2006) with an A-EB-Bt horizon sequence, in which clays undergo a translocation process from surface to deep horizons. The very low reaction (pH 4.5–5.4) of these soils is due to the removal of carbonates and bases by infiltrating water. On steep wooded slopes, where rocky outcrops are often widespread, very thin soils of the Epileptic Phaeozems (Calcaric) (IUSS 2007) can be found. These soils are characterized by a high skeleton and organic matter content in the A horizon. On moderately steep wooded slopes characterized by evident karst phenomena, soils with an A-Bt-R profile are present. These soils are thicker than the previous ones but do not exceed 75 cm in any case.

Dataset

We used 25 relevés collected by the authors between 2021 and 2023. All the relevés were carried out according to the 7-step version of the cover-abundance scale of Braun-Blanquet (1964), which was transformed into central class percentage values (r=0.1%, +=0.5%, 1=3%, 2=15%, 3=37.5%, 4=62.5%, 5=87.5%) for statistical analysis. The location of the plots was chosen based on the experimental plots of the LIFE SPAN project, which selected 25 forest plots randomly distributed within the forest and reachable via forest roads. The plot is composed of five circular subplots with a radius of 4 m, strategically positioned: one at the center of the plot and the others placed 12 m apart (center to center) in the directions of 45°, 135°, 225°, and 315°. The total area sampled is approximately 250 m^2. Details of relevés data are presented in Suppl. material 1.

The dataset is composed of three types of matrices: floristic (25 relevés × 94 species), environmental parameters (6 variables × 25 relevés), and indicators matrix (8 variables × 94 species). The environmental parameters matrix comprises variables collected in the field, such as altitude, aspect, slope, percentage of surface rockiness, percentage of tree layer and herbaceous layer cover. The indicators matrix includes Ellenberg indicator values (EIVs) for light, temperature, moisture, soil reaction, and nitrogen (Tichý et al. 2023) and other categories such as phytosociological units at class level (Mucina et al. 2016), chorotypes (Pignatti et al. 2017), and life forms (Dřevojan et al. 2023).

The syntaxonomic reference for diagnostic species of beech forests follows Willner et al. (2017).

Data analysis

Initially, we calculated the average of EIVs weighted on species cover, and the relative percentage cover of each phytosociological unit, chorotype and life-form for each relevé.

The different communities were identified by performing an agglomerative cluster analysis on a Bray-Curtis (Faith et al. 1987; Ricotta and Podani 2017) dissimilarity matrix using Ward's algorithm (Murtagh and Legendre 2014) with the *stats* package (R Core Team 2022). We applied a nonmetric multidimensional scaling (NMDS) ordination (*vegan* package, Oksanen et al. 2016) and identified the gradients of variables involved using the *envfit* function, which fits supplementary variables on ordination scores using multiple regression. Significance of each variable was tested using a permutation test (n = 999) and only significant variables have been plotted (p-value < 0.05). The *indicspecies* package (De Cáceres and Legendre

2009) was used to determine the fidelity between species and clusters by Pearson's *phi* coefficient of association (Chytrý et al. 2020). We applied the phi coefficient equalizing clusters size (Tichý and Chytrý 2006) after transforming our floristic matrix to presence-absence data. A species was determined as diagnostic if it had phi > 0.5, a statistically significant association with a particular cluster (p-value < 0.05), and a constancy value equal to or higher than 30%. (Suppl. material 2)

Finally, in order to compare the means of variables between clusters, we performed one-way ANOVA and multiple pairwise-comparisons by Tukey HSD on the variables, respecting the assumptions of normality by Shapiro-Wilk test and homogeneity by Levene's test. When assumptions were not accomplished, we applied the Kruskal-Wallis rank sum test and multiple pairwise-comparisons by Dunn's test with Bonferroni correction for p-value.

All analyses and graphics were performed using R software (R Core Team 2022).

Results

The results of the cluster analysis carried out on the floristic matrix show two main groups of relevés (Figure 4a): the first cluster (A) represents the *Picea abies* community, while the second cluster represents the *Fagus sylvatica* forest and is divided into two sub-clusters. The first sub-cluster (B1) is the mixed *Fagus sylvatica* and *Abies alba* community, while the second (B2) is the almost pure *Fagus sylvatica* community.

In the NMDS diagram (Figure 4b), the three clusters do not overlap, and the projections of variables by *envfit* function show several significant correlations with the ordination axes. The first axis is mainly correlated with EIVs of light, temperature, and moisture, as well as with the *Carpino-Fagetea sylvaticae* and *Vaccinio-Piceetea* classes. It is also weakly correlated with altitude, with Central European, Euro-Asian, and Circumboreal chorotypes, as well as with Hemicryptophyte life form.

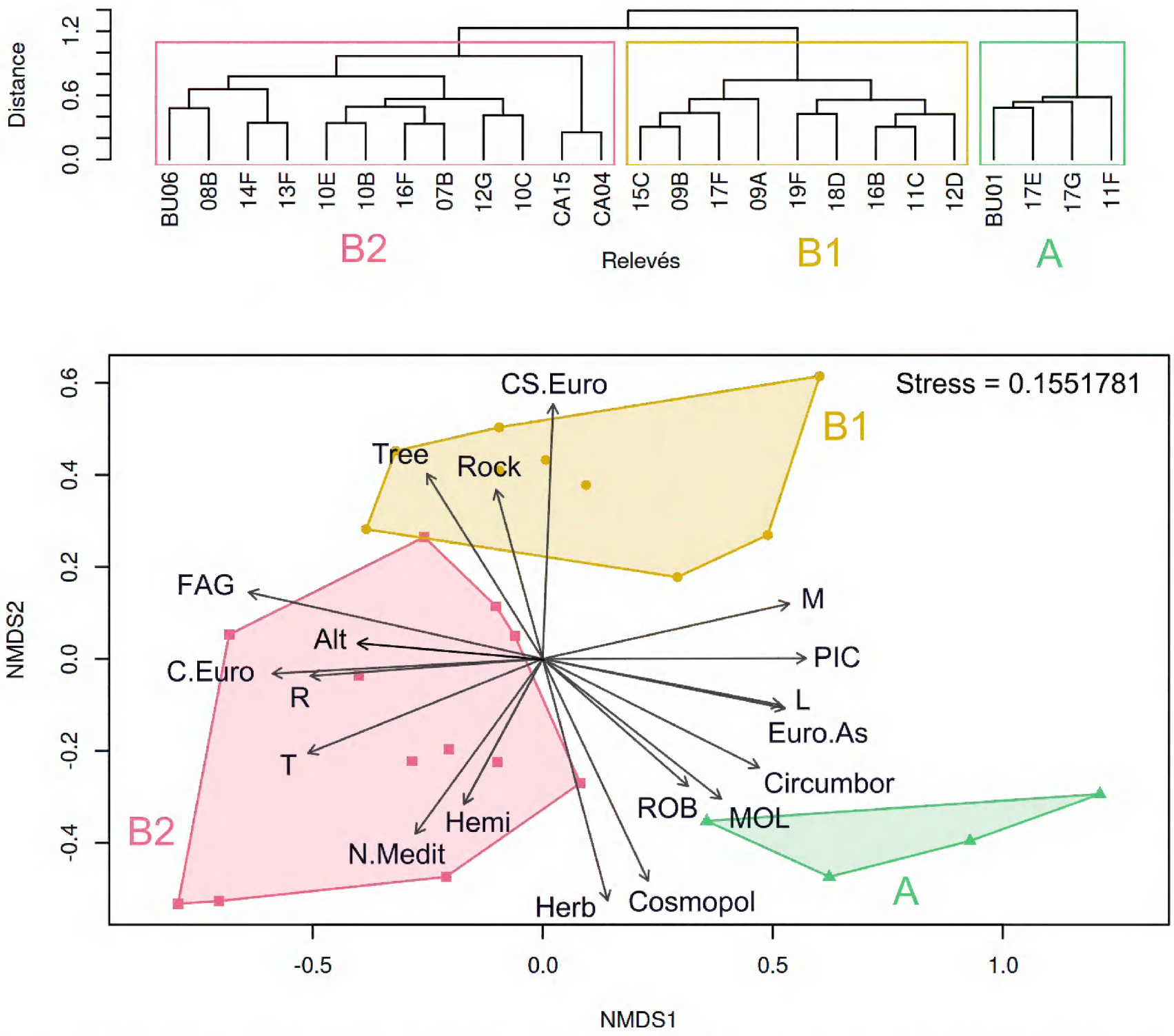

Figure 4. a) Dendrogram of relevés resulting from Ward's minimum variance clustering, with Bray-Curtis distance and **b)** NMDS ordination diagram. Cluster **A** *Picea abies* community. Cluster **B1** *Fagus sylvatica* with *Abies alba* community. Cluster **B2** *Fagus sylvatica* community. Overlaid vectors represent the following variables: EIVs **L** light, **T** temperature, **M** moisture, **R** soil reaction, **FAG** *Carpino-Fagetea sylvaticae*, **PIC** *Vaccinio-Piceetea*, **MOL** *Molinio-Arrhenatheretea*, **ROB** *Robinietea*, **C.Euro** Central European, **Euro.As** Euro-Asian, Circumboreal, **CS.Euro** Central-South European, **N.Medit** North-Mediterranean, **Cosmopol** Cosmopolite, **Hemi** Hemicriptophyte, **Tree** tree layer cover, **Herb** herb layer cover, **Rock** rockiness, **Alt** altitude.

The second axis is mainly correlated with Central-South European and Cosmopolites chorotypes, as well as with the percentage of tree layer, herb layer, and rockiness. It is also weakly correlated with the North-Mediterranean chorotype and *Molinio-Arrhenatheretea* and *Robinietea* phytosociological classes.

From the ordination, the effect of thermal inversion is clearly visible, which places the relevés of A at the lower altitude, with higher EIV of moisture, and the relevés of B2 with higher EIV of temperature, at the top. Another gradient is the phytogeographical one, which orders the relevés according to three directions: in cluster A they are predominantly Circumboreal and Euro-Asian chorotypes, rich in *Vaccinio-Piceetea* species, while in sub-cluster B1 they comprise the Central-South European chorotype and in sub-cluster B2 the Central European chorotype with *Carpino-Fagetea sylvaticae* species and thermophile species from the North of Mediterranean.

Description of clusters and communities

Details of cluster species composition are presented in Suppl. material 2.

Cluster A: Picea abies community (Figure 5)

Diagnostic species of herb layer: *Alchemilla xanthochlora*, *Chaerophyllum hirsutum*, *Hypericum montanum*, *Maianthemum bifolium*, *Myosotis sylvatica*, *Phegopteris connectilis* and *Scrophularia nodosa*.

In the first cluster, *Picea abies* reaches the highest cover and frequency. These relevés are located at an average altitude of 1135 m a.s.l., with relevés 17E and 17G on the edge of the Cansiglio plateau where this community mainly develops, while relevés 11F and B01 are found inside the forest in areas with spruce afforestation. Cluster A is characterized by the lowest EIVs of temperature and soil reaction, and the highest values of moisture and light (Figure 6).

The tree layer is more open, and the herbaceous layer has the maximum cover percentage and the largest number of species, with most of them being Hemicryptophytes. Regarding the chorological spectrum, Circumboreal, Euro-Asian, South-East European, and Cosmopolite species reach the highest values, while Central European and Central-South European species have the lowest values (Table 1).

One of the most frequent diagnostic species is *Chaerophyllum hirsutum*, which, together with mosses, forms a carpet favoured by high moisture. These conditions also favour the growth of *Alchemilla xanthochlora*, *Maianthemum bifolium*, *Myosotis sylvatica*, and *Phegopteris connectilis*, which prefers this acidic substrate. Where the canopy is even more open or towards the fringes, *Hypericum montanum* and *Scrophularia nodosa* occur, especially in the areas often used by ungulates to forage or breed (relevés 17E, 17G). Although in this community *Vaccinio-Piceetea* species reach the highest frequency, the higher abundances correspond to *Carpino-Fagetea sylvaticae* species; furthermore, *Molinio-Arrhenatheretea* and *Robinietea*

Figure 5. *Picea abies* community. **Top-left**: *Phegopteris connectilis* **Bottom-left**: *Maianthemum bifolium*. **Right side:** relevé 17E on the bottom of Cansiglio plateau.

Table 1. Means and standard deviation of environmental parameters and relative cover as percentage of phytosociological units, chorotypes and life forms. **A** *Picea abies* community. **B1** *Fagus sylvatica* with *Abies alba* community. **B2** *Fagus sylvatica* community. Chi-squared resulting from Kruskal-Wallis test and the letters express the significance of the differences between group means from pairwise comparisons by Dunn test. Only variables with values > 1 for at least one cluster are displayed.

Cluster	**A**		**B1**		**B2**			
Number of sampling sites	**4**		**8**		**13**			
	Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**	***chi*-squared**	***p*-value**
Environmental parameters								
Altitude (m a.s.l.)	1134.5	226.0	1195.1	98.8	1218.9	110.5	0.26734	0.875
Aspect (°)	285.5	42.4	217.8	105.5	230.4	103.6	1.3819	0.501
Slope (°)	18.8	13.1	30.0	8.9	27.7	8.1	1.7814	0.410
Tree cover layer (%)	55.8 a	12.3	97.9 b	12.4	79.6 a	8.8	16.048	0.000 ***
Herb cover layer (%)	85.8 b	17.9	25.0 a	24.8	52.5 ab	22.7	10.774	0.005 **
Rockiness (%)	0.0 a	0.0	10.0 b	7.5	4.4 ab	4.1	9.8493	0.007 **
Phytosociological units								
Carpino-Fagetea sylvaticae	47.3 b	20.03	81.5 a	18.76	93.0 a	6.22	17.08	0.000 ***
Molinio-Arrhenatheretea	10.7 a	7.66	0.0 b	0.02	0.2 b	0.51	11.201	0.004 **
Robinietea	5.4 a	7.78	0.1 b	0.17	1.2 ab	1.23	4.267	0.027 *
Vaccinio-Piceetea	34.0 a	23.36	16.9 ab	19.20	4.5 b	5.52	6.773	0.005 **
Chorotypes								
Central South European	0.00 a	0.00	28.17 b	18.46	3.63 a	6.53	15.109	0.001 ***
Circumboreal	27.9 b	8.93	8.7 a	9.37	6.9 a	6.53	11.29	0.000 ***
Cosmopolite	11.03 a	8.12	0.54 b	0.65	4.05 ab	3.99	10.93	0.004 **
Euro Asian	25.02 b	10.85	10.56 a	12.15	4.53 a	4.19	8.903	0.001 **
Euro Central	8.66 a	12.41	37.31 ab	23.20	55.40 b	12.41	12.59	0.000 ***
Nord Mediterranean	0.00	0.00	0.00	0.00	3.72	8.10	3.0064	0.222
Orophite South European	1.58	2.98	0.48	0.96	0.10	0.35	2.5707	0.277
Paleotemprate	1.05 b	1.03	0.22 a	0.57	0.07 a	0.23	8.0099	0.018 *
South East European	20.00	12.84	8.54	4.83	15.16	10.92	2.0572	0.358
South European	0.01	0.02	3.33	5.04	2.08	4.35	1.4934	0.474
South West European	4.49	2.55	1.81	2.53	3.77	5.39	2.1573	0.340
Life forms								
Geophyte	0.23 a	0.42	5.13 ab	4.58	12.03 b	9.87	10.473	0.005 **
Hemicryptophyte	70.28 b	8.64	19.45 a	5.22	26.91 a	6.75	11.038	0.004 **
Phanerophyte	29.44 a	11.76	74.78 b	15.12	60.06 ab	9.83	13.51	0.001 **

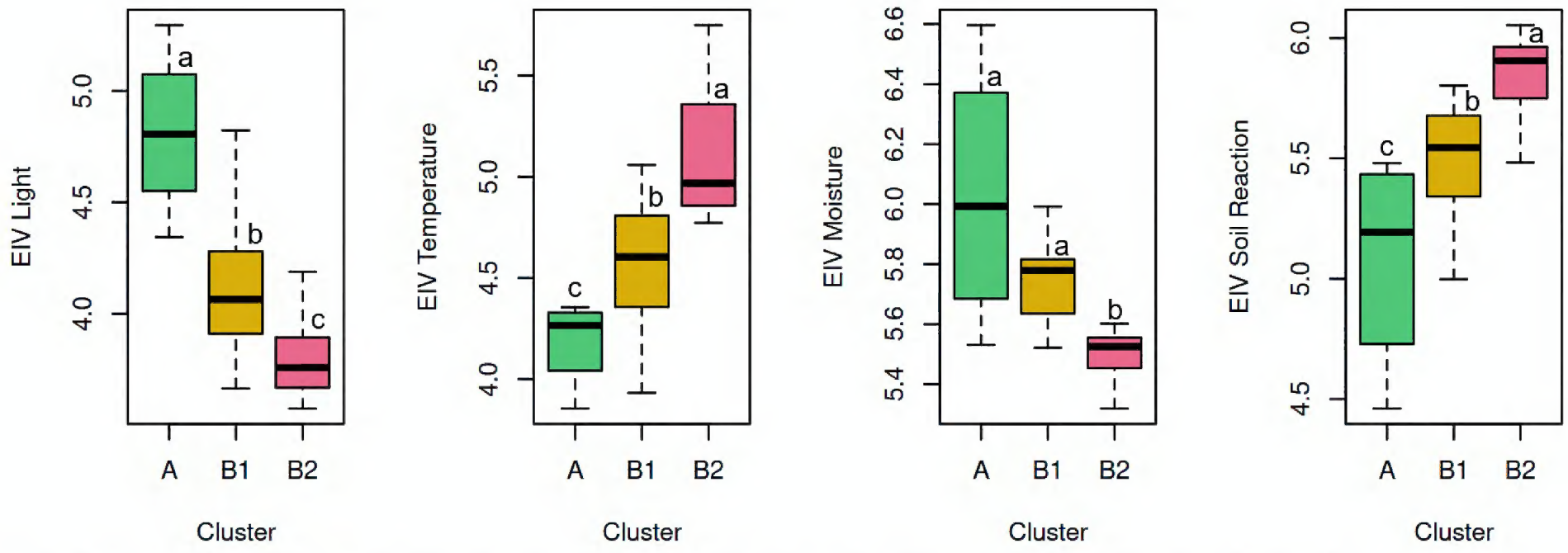

Figure 6. EIVs for light, temperature, moisture and soil reaction for each cluster. Y-axis: values of the EIVs. X-axis: A *Picea abies* community, B1 *Fagus sylvatica* with *Abies alba* community, B2 *Fagus sylvatica* community. Box plots of median, interquartile range and range with different letters express the significance of the differences between group means at $p < 0.05$ according to Tukey's test following a significant ANOVA.

species also occur, due to the position of these relevés close to the grasslands and to the most anthropized part of the study area (Table 1).

Finally, we looked for cluster differences concerning the number of diagnostic species of beech forests indicated by Willner et al. (2017). We found that there are very few species diagnostic of *Aremonio-Fagion*, including the suballiance *Lonicero alpigenae-Fagenion*; however, the number of meso-basiphytic beech forest species remains similar to that of cluster B (Figure 7).

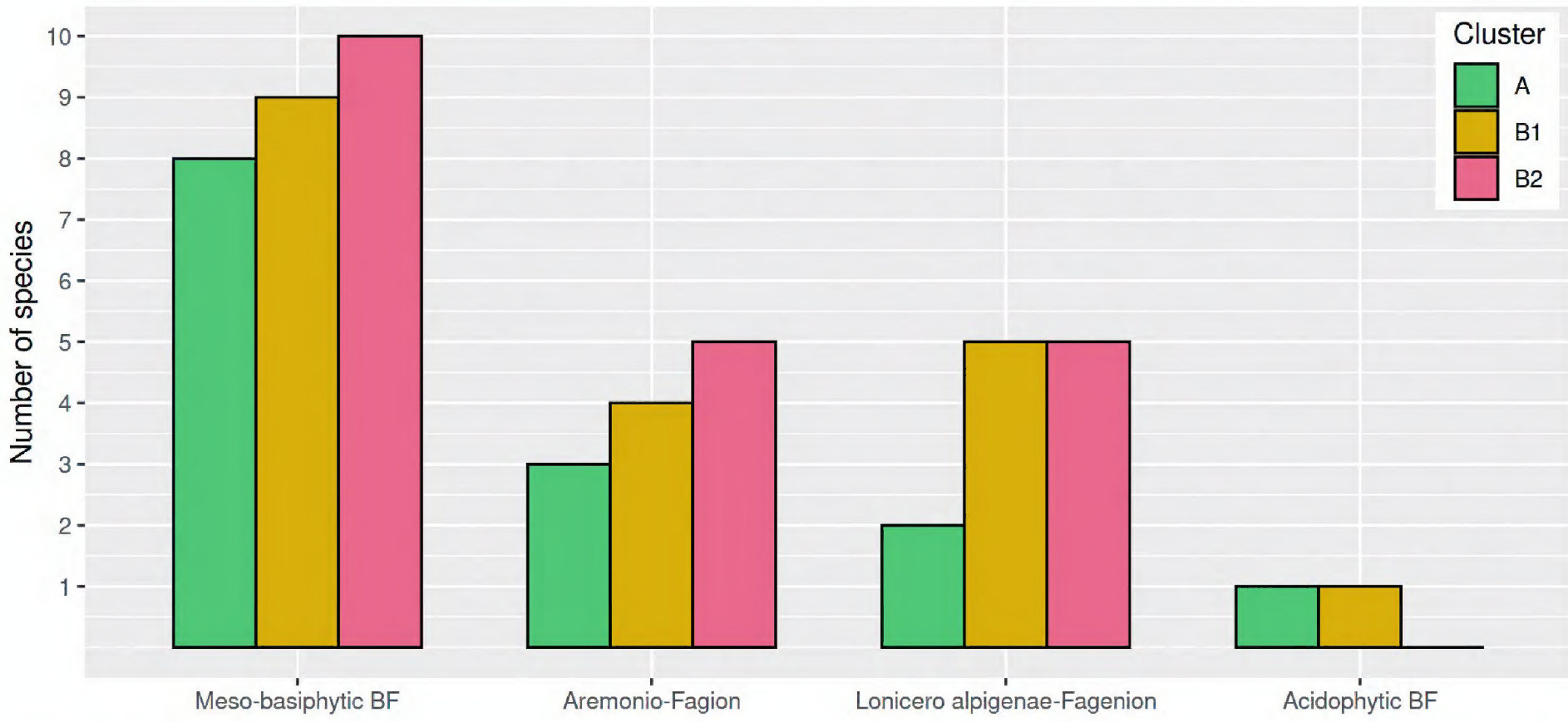

Figure 7. Number of beech diagnostic species according to Willner et al. (2017). X-axis: main groups of diagnostic species for each cluster. Cluster A *Picea abies* community. Cluster B1 *Fagus sylvatica* with *Abies alba* community. Cluster *B2 Fagus sylvatica* community.

Cluster B1: Fagus sylvatica with Abies alba community (Figure 8)

Diagnostic species of herb layer: *Circaea alpina*.

The second cluster consists of eight relevés in which the tree layer is a mixture of *Fagus sylvatica*, *Abies alba*, and sometimes *Picea abies*. These relevés show a greater closure of the canopy and a lower cover of the herbaceous layer in which *Cardamine trifolia* and *Anemone trifolia* achieve the greatest cover and frequency and resulting in *Circaea alpina* being diagnostic. The relevés are positioned mainly on the steepest and rockiest slopes at an average altitude of 1185 m a.s.l. EIVs are intermediate between the other two groups, with significant differences in light, temperature and reaction (Figure 6). Central European species represent the main chorotype, followed by the Central-South European and Euro-Asian ones. The preponderant phytosociological group is the *Carpino-Fagetea*, as for sub-cluster B2, while the species of the *Vaccinio-Piceetea* decrease to about 17% (Table 1).

Cluster B2: pure Fagus sylvatica community (Figure 9)

Diagnostic species of herb layer: *Lathyrus venetus*.

The last cluster is composed of 13 relevés of almost pure *Fagus sylvatica* stands, where *Cardamine pentaphyllos*, *C. enneaphyllos* and *Geranium nodosum* reach maximum cover and frequency. *Lathyrus venetus* occurs as a diagnostic, but it reaches low frequency (31%). This community is present mainly at the top of the massif at an average altitude of 1228 m a.s.l., on Western facing slopes. EIVs for temperature and soil reaction reach the highest values but are lower for moisture and light (Figure 6). The chorological spectrum shows that Central European species predominate, followed by the South-Eastern, then less the Circumboreal, Cosmopolite and the other European species. As for the phytosociological groups, it is almost entirely *Carpino-Fagetea*, with a small percentage of *Vaccinio-Piceetea* (Table 1).

Discussion

Although *Vaccinio-Piceetea* species are most abundant in the *Picea abies* community, the most represented phytosociological group remains the *Fagetalia*. This is common in the *Picea abies* forests of the mountain belt of the Alps. Many of these forests in Friuli originated from beech forests that were converted to spruce forests through silvicultural practices (Poldini and Bressan 2007), although thermal inversion may suggest a natural component in the case of Cansiglio (Pignatti 1998). This results in a difficult syntaxonomic classification, particularly in higher syntaxonomic levels where these montane communities, particularly in areas supporting *Galium odoratum*, are sometimes attributed to the order *Fagetalia* (Leuschner and Ellenberg 2017). The presence of *Milium effusum*, *Ranunculus lanuginosus*, *R. platanifolius*, *Saxifraga rotundifolia*, *Senecio cacaliaster*, and *Stellaria nemorum* could lead to the classification of this community as the association *Senecioni cacaliaster-Piceetum* described by Poldini and Bressan (2007) for the forests of Friuli. These are the mountain spruce forests, particularly rich in megaforbs, that are distributed mainly in the calcareous and dolomitic bedrocks of Carnic Alps (Poldini 1989) on acidic Distric Cambisol and arenitic substrates. Further surveys are needed to investigate the soil features in detail.

The mixed *Fagus sylvatica* with *Abies alba* community mainly develops on the cooler inner Northern slope characterised by stone blocks that favour cold ventilation. The herb layer is poor and characterised by the high frequency of *Oxalis acetosella* and enriched by Illyrian species such as *Anemone trifolia* and *Cardamine trifolia*. A diagnostic species of this mixed forest is *Circaea alpina*, transgressive from the *Vaccinio-Piceetea*, and indicated as a local differential species of the *Abieti-Piceion* by Poldini and Nardini (1993), which attests to its fresh character compared to the pure *Fagus sylvatica* forest, confirmed by EIVs differences.

Figure 8. Mixed *Fagus sylvatica* with *Abies alba* community. **Left side:** relevé 16F on the steepest side of Cansiglio forest. **Top-right**: *Circaea alpina*. **Bottom-right**: *Cardamine trifolia*.

Figure 9. Pure *Fagus sylvatica* community. **Top-left**: *Lathyrus venetus*. **Bottom-left**: *Cardamine pentaphyllos*. **Right side:** relevé 7B on the top of the Cansiglio forest.

Finally, the pure *Fagus sylvatica* community is found in the highest belt, where the influence of warm and humid currents from the Friulan-Venetian plain favours optimal growing conditions for the beech. This community can be identified as the formerly so-called 'high-mountain beech forest with *Dentaria* spp.' (Poldini and Nardini 1993) which is established on deep soils rich in organic matter and skeleton, and is mainly characterised by the presence of mesophilic and hygromorphic species, transgressive from megaforb formations. The herb layer is almost entirely composed of beech forest species, including Illyrian species such as *Cardamine enneaphyllos*, *C. pentaphyllos*, *Geranium nodosum*, and *Lamium orvala*.

Considering the similarity of the floristic composition and the scarcity of diagnostic species, we may consider the mixed silver fir-beech forest as a facies expressing an ecological differentiation of the *Cardamino pentaphylli-Fagetum* Mayer and Hofmann 1969 *fagetosum* Poldini and Nardini 1993, rather than a separate association such as *Cardamino pentaphylli-Abietetum* Mayer 1974, as described for Cansiglio by Gafta (1994) and reported by Poldini and Bressan (2007) for FVG.

At the syntaxonomic level, both the pure beech forest and the silver fir-beech mixed forest can be placed within the meso-basiphytic beech forests, according to the ecological subdivision of European beech forests by Willner et al. (2017), due to the presence of *Actaea spicata*, *Cardamine bulbifera*, *Carex sylvatica*, *Galium odoratum*, *Geranium robertianum*, *Impatiens noli-tangere*, *Lamium galeobdolon*, *Paris quadrifolia*, and *Scrophularia nodosa*. Considering the importance of the phytogeographical and evolutionary issues which characterise the communities in the Eastern side of the Alps and Prealps, in this case, we choose to adopt the phytogeographical subdivision in Willner et al. (2017) and attribute this community to the *Aremonio-Fagion* alliance, thanks to the presence of Illyrian species such as *Adenostyles alpina*, *Anemone trifolia*, *Aposeris foetida*, *Cardamine enneaphyllos* and *Cyclamen purpurascens*. Regarding the suballiance, the presence of *Asplenium viride*, *Cardamine trifolia*, *Homogyne alpina*, *Lonicera nigra*, *Petasites albus*, *Rosa pendulina* and *Veronica urticifolia* places them within the *Lonicero alpigenae-Fagenion*, which includes the *Saxifrago rotundifoliae-Fagenion* proposed by Marinšek et al. (2013) for calcareous soils and described by Poldini and Nardini (1993) for Friuli-Venezia Giulia.

Conclusion

The vegetation of the Cansiglio forest has distinctive characteristics due to various factors, such as karst geomorphology, geographic location, evolution of glacial cover since the last glaciation, and human intervention. The most striking aspect is the karst geomorphology, which is characterized by a closed inner plateau surrounded by a steep mountain crown, resulting in a phenomenon of thermal inversion. This causes a stagnation of cold, moist air, which favours the growth of *Picea abies* at the bottom, although the long history of forest management has also contributed to the establishment of this community. This community could be identified as the *Senecioni cacaliaster-Piceetum* first described by Poldini and Bressan (2007) for the forests of FVG but, due to the scarcity of relevés for this group, further surveying is needed to deepen the knowledge of this community.

Pure and mixed beech stands can be identified as the *Cardamino pentaphylli-Fagetum fagetosum*, with an *Abies alba* facies on cool, Northern slopes, which takes on the physiognomy of the '*Abieti-Fagetum*'. Willner's flexible syntaxonomic approach (Willner et al. 2017) allows us to give importance to the phytogeographical and evolutionary issues and to include these communities in the *Aremonio-Fagion* alliance and the *Lonicero alpigenae-Fagenion* suballiance.

Data availability

Data are included in the electronic appendices.

Author contributions

B.D., F.F., P.C. and F.S. planned the research, F.S. conducted the field sampling, performed the statistical analyses and wrote the text, while all authors critically revised the manuscript.

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References

ARPAV- Regional Agency for Environmental Prevention and Protection of the Veneto (2023) Centro Metereologico Variabili meteorologiche [Center for Metereological variables] 1994–2022. https://www.arpa.veneto.it/temi-ambientali/meteo [accessed 20 Jan 2023]

Braun-Blanquet J (1964) Pflanzensoziologie. Grundzüge der Vegetationskunde. 3rd ed. Springer, Wien, AT. https://doi.org/10.1007/978-3-7091-8110-2

Busato PA, Lorenzoni GG (1973) Considerazioni sull'inversione di vegetazione nelle depressioni del Cansiglio (Prealpi Venete), Atti del III Convegno sulla storia naturale delle Prealpi Venete [Considerations on vegetation inversion in the Cansiglio depressions (Veneto Prealps), Proceedings of the 3rd Conference on the Natural History of the Venetian Prealps]. Bollettino del Museo Civico di Storia Naturale di Venezia 24: 75–81.

Cassol M, Borgo A, Genero F, Scariot A (2013) Relazione del Piano di gestione area della rete Natura 2000 SIC IT3310006 Foresta del Cansiglio [Natura 2000 Network Area Management Plan Report SIC IT3310006 Cansiglio Forest]. Autonomous Region of Friuli Venezia Giulia, Udine, IT, 343 pp.

Chiapella Feoli L, Poldini L (1993) Prati e pascoli del Friuli (NE Italia) su substrati basici [Meadows and pastures in Friuli (NE Italy) on basic substrates]. Studia Geobotanica 13: 3–140.

Chytrý M, Tichý L, Hennekens SM, Knollová I, Janssen JAM, Rodwell JS, Peterka T, Marcenò C, Landucci F, … Schaminée JHJ (2020) EUNIS Habitat Classification: expert system, characteristic species combinations and distribution maps of European habitats. Applied Vegetation Science 23: 648–675. https://doi.org/10.1111/avsc.12519

De Cáceres M, Legendre P (2009) Associations between species and groups of sites: Indices and statistical inference. Ecology 90: 3566–3574. https://doi.org/10.1890/08-1823.1

Del Favero R, Poldini L, Bortoli PL, Dreossi G, Lasen C, Vanone G (1998) La vegetazione forestale e la selvicoltura nella regione Friuli-Venezia Giulia [Forest vegetation and silviculture in the Friuli-Venezia Giulia region]. Regione Autonoma Friuli Venezia Giulia, Direzione Regionale delle Foreste, Udine, IT, 793 pp.

Dřevojan P, Čeplová N, Štěpánková P, Axmanová I (2023) Life form. https://floraveg.eu/ [accessed 20 Jan 2023]

Euro+Med (2023) The Euro+Med PlantBase – the information resource for Euro-Mediterranean plant diversity. https://ww2.bgbm.org/EuroPlusMed/ [accessed 20 Jan 2023]

Faith DP, Minchin PR, Belbin L (1987) Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69: 57–68. https://doi.org/10.1007/BF00038687

Gafta D (1994) Tipologia, sinecologia e sincorologia delle abetine nelle Alpi del Trentino [Typology, synecology and synchorology offir forests in the Trentino Alps]. [Braun-Blanquetia, Review of geobotanical monographs 12]. Camerino, IT, 69 pp.

Garlato A, Borsato V (2016) I suoli del SIC-ZPS IT3230077 "Foresta del Cansiglio"(NE-Italia) [The soil of SIC-ZPS IT3230077 "Foresta del Cansiglio"(NE-Italy)]. Lavori Società Veneziana di Science Naturali 41: 115–120.

Hofmann A (1931) L'assestamento della foresta demaniale del Cansiglio [Management of the Cansiglio State Forest]. L'Alpe, Rivista Forestale Italiana, 4: 201–208.

IUSS Working Group WRB (2007) World Reference Base for Soil Resources 2006, first update 2007. [World Soil Resources Reports No. 103]. FAO, Rome, IT.

Leuschner C, Ellenberg H (2017) Ecology of Central European Forests. Springer, Cham, CH, 972 pp. https://doi.org/10.1007/978-3-319-43042-3

Magri D, Vendramin GG, Comps B, Dupanloup I, Geburek T, Gömöry D, Latalowa M, de Beaulieu JL (2006) A new scenario for the Quaternary history of European beech populations: Palaeobotanical evidence and genetic consequences. The New Phytologist 171: 199–221. https://doi.org/10.1111/j.1469-8137.2006.01740.x

Mantovani F, Panizza M, Semenza E, Piacente S (1976) L'Alpago (Prealpi Bellunesi), Geologia, Geomorfologia, Nivopluviometria [The Alpago (Belluno Prealps), Geology, Geomorphology, Nivopluviometry]. Bollettino della Società Geologica Italiana 95: 1589–1656.

Marinček L, Mucina L, Zupančič M, Poldini L, Dakskobler I, Accetto M (1993) Nomenklatorische Revision der illyrischen Buchenwälder. Studia Geobotanica 12: 121–135.

Marinšek A, Šilc U, Čarni A (2013) Geographical and ecological differentiation of *Fagus* forest vegetation in SE Europe. Applied Vegetation Science 16: 131–147. https://doi.org/10.1111/j.1654-109X.2012.01203.x

Mason F, Di Salvatore U, Zapponi L, Cantiani P, De Cinti B, Ferretti F (2016) Ilots de Senescence in the ManFor C.BD sites. Italian Journal of Agronomy 11: 1–175.

Mayer H, Hofmann A (1969) Tannenreiche Walder am Sudabfall der mittleren Ostalpen. BLV Verlagsgesellschaft, München, DE, 259 pp.

Mucina L, Bültmann H, Dierßen K, Theurillat J-P, Raus T, Čarni A, Šumberová K, Willner W, Dengler J, … Tichý L (2016) Vegetation of Europe: Hierarchical floristic classification system of plant, lichen, and algal communities. Applied Vegetation Science 19(suppl. 1): 3–264. https://doi.org/10.1111/avsc.12257

Murtagh F, Legendre P (2014) Ward's hierarchical agglomerative clustering method: Which algorithms implement Ward's criterion? Journal of Classification 31: 274–295. https://doi.org/10.1007/s00357-014-9161-z

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2016) vegan: community ecology package. R package version 2.4-2. https://cran.r-project.org/web/packages/vegan/index.html [accessed 20 Jan 2023]

OpenStreetMap contributors (2015) Planet dump. https://planet.openstreetmap.org [accessed 20 Jan 2023]

Pignatti S (1998) I boschi d'Italia: sinecologia e biodiversità [The forests of Italy: synecology and biodiversity]. 1st ed. UTET, Torino, IT, 676 pp.

Pignatti E, Pignatti S (2016) Plant life of the Dolomites. Vegetation structure and ecology [Publication of the Museum of Nature South Tyrol 8]. Springer, Heidelberg, DE, 1347 pp. https://doi.org/10.1007/978-3-662-48032-8

Pignatti S, Guarino R, La Rosa M (2017) Flora d'Italia [Flora of Italy]. Edagricole, Milano, IT, 1120 pp.

Poldini L (1989) La suddivisione fitogeografica del Friuli-Venezia Giulia [The phytogeographical subdivision of Friuli-Venezia Giulia]. Biogeographia - The Journal of Integrative Biogeography 13: 41–56. https://doi.org/10.21426/B613110289

Poldini L, Bressan E (2007) I boschi ad abete rosso ed abete bianco in Friuli (Italia nord-orientale) [Spruce and fir forests in Friuli (North-Eastern Italy)]. Fitosociologia 44(2): 15–54.

Poldini L, Galizia Vuerich L (1997) Irradiazioni di vegetazioni illiriche nelle Alpi sud-orientali e loro avanterra [Irradiation of illyric vegetation in the South-Eastern Alps and their forelands]. Proceedings of the 2nd conference on alpine ecology and biogeography. Histoire et Nature 51: 195–210.

Poldini L, Nardini S (1993) Boschi di forra, faggete e abieteti in Friuli (NE Italia) [Gorge forests, beech and fir forests in Friuli (NE Italy)]. Studia Geobotanica 13: 215–298.

Poldini L, Vidali M (1993) Prospetto sistematico della vegetazione nel Friuli Venezia Giulia [Systematic overview of vegetation in Friuli Venezia Giulia]. Atti dei convegni dei Lincei "La vegetazione italiana" 115: 155–174.

R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, AT. https://www.R-project.org/ [accessed 20 Jan 2023]

Ricotta C, Podani J (2017) On some properties of the Bray-Curtis dissimilarity and their ecological meaning. Ecological Complexity 31: 201–205. https://doi.org/10.1016/j.ecocom.2017.07.003

Tichý L, Chytrý M (2006) Statistical determination of diagnostic species for site groups of unequal size. Journal of Vegetation Science 17: 809–818. https://doi.org/10.1111/j.1654-1103.2006.tb02504.x

Tichý L, Axmanová I, Dengler J, Guarino R, Jansen F, Midolo G, Nobis MP, Van Meerbeek K, Aćić S, … Chytrý M (2023) Ellenberg-type indicator values for European vascular plant species. Journal of Vegetation Science 34: e13168. https://doi.org/10.1111/jvs.13168

Tinner W, Lotter AF (2006) Holocene expansions of *Fagus silvatica* and *Abies alba* in Central Europe: Where are we after eight decades of debate? Quaternary Science Reviews 25: 526–549. https://doi.org/10.1016/j.quascirev.2005.03.017

Trinajstić I (1992) A contribution to the phytogeographical classification of the Illyrian floral element. Acta Botanica Croatica 51(1): 135–141.

Vescovi E, Ravazzi C, Arpenti E, Finsinger W, Pini R, Valsecchi V, Wick L, Ammann B, Tinner W (2007) Interactions between climate and vegetation during the Lateglacial period as recorded by lake and mire sediment archives in Northern Italy and Southern Switzerland. Quaternary Science Reviews 26: 1650–1669. https://doi.org/10.1016/j.quascirev.2007.03.005

Vitale A, San Martini P (1914) Uno sguardo alla gestione della foresta demaniale del Cansiglio [A look at the management of the Cansiglio State Forest]. L'Alpe, Rivista Forestale Italiana series II, 9: 292–299.

Willner W, Di Pietro R, Bergmeier E (2009) Phytogeographical evidence for post-glacial dispersal limitation of European *Fagus sylvatica* forest species. Ecography 32: 1011–1018. https://doi.org/10.1111/j.1600-0587.2009.05957.x

Willner W, Jiménez-Alfaro B, Agrillo E, Biurrun I, Campos JA, Čarni A, Casella L, Csiky J, Ćušterevska R, … Chytrý M (2017) Classification of European *Fagus sylvatica* forests: A Gordian Knot? Applied Vegetation Science 20: 494–512. https://doi.org/10.1111/avsc.12299

E-mail and ORCID

Flavia Sicuriello (Corresponding author, flavia.sicuriello@cnr.it), ORCID: https://orcid.org/0000-0002-0337-2147
Fabrizio Ferretti (fabrizio.ferretti@crea.gov.it), ORCID: https://orcid.org/0000-0002-0604-5336
Paolo Colangelo (paolo.colangelo@cnr.it), ORCID: https://orcid.org/0000-0002-0283-3618
Bruno De Cinti (bruno.decinti@cnr.it), ORCID: https://orcid.org/0000-0002-7277-6081

Supplementary material

Supplementary material 1
Dataframe of relevés (*.xlsx)
Link: https://doi.org/10.3897/VCS.118821.suppl1

Supplementary material 2
Synoptic table of relevés (*.xlsx)
Link: https://doi.org/10.3897/VCS.118821.suppl2